"The Ascent of Water in Trees." By ALFRED J. EWART, D.Sc., Ph.D., F.L.S., Lecturer on Botany in the University of Birmingham. Communicated by FRANCIS DARWIN, For. Sec. R.S. Received November 2,—Read December 1, 1904.

(Abstract.)

As the result of a series of experimental observations bearing upon this problem, the author has been led to the conclusions stated in brief below.

The flow of water through open vessels filled with sap takes place in accordance with Poiseuille's formula for the flow through rigid cylindrical tubes, divergences being due to the presence of irregular internal thickenings in the vessels, and to local constrictions or deviations from the circular outline.

Hence the velocity of flow is directly proportional to the pressure and to the square of the radius of the tube, inversely proportional to the length of the tube and to the viscosity of the liquid. A small number of large vessels, therefore, offer very much less resistance to flow than a large number of narrow ones having the same length, and the same total internal area of cross-section. Since viscosity is largely dependent upon temperature, the latter forms an important factor in regulating the flow, the viscosity and the resistance falling with a rise of temperature.

With an average rate of flow the total resistance due to the viscosity of the water flowing through the vessels is always less, and in climbing plants with large vessels is considerably less, than a head of water equal in height to the stem. The adult vessels of actively transpiring Angiospermous trees always contain air-bubbles, and these introduce a resistance to flow which is inversely proportional to the radius of the tube, when the air-bubbles and water-columns move together. When the air-bubbles are comparatively stationary, as in most vessels, the resistance is still further increased, and it becomes very great when the vessels are small and the air-bubbles numerous. In intact vessels containing air the rates of flow under similar pressures are proportional to a power of the radius lying between 1 and 2, the volume passing to a power of the radius lying between 2 and 4.

Estimations of the amount of flow, made from the rate of flow and the diameters and number of the vessels, showed that the actual flow takes place in the wood of Dicotyledons almost entirely through the cavities of the vessels and hardly at all through the tracheides. In young stems saturated with water under pressure, a considerable flow takes place through the pith, but practically none in intact transpiring stems.

In a cut stem, apart from the blocking at the cut surfaces, a gradual diminution of conductivity occurs along its entire length after water has been passed through for some time. This appears, in part at least, to be due to the development of micro-organisms in the vessels, but may be aided by swelling, by lessened permeability, or by other changes in their walls.

The length of the vessels in the wood of the branches examined averages from 7 to 36 centimetres, the tracheides of the yew being from 0·2 to 0·5 of a centimetre in length. Since, however, the vessels appear mainly to end at the nodes where branches arise, it is possible that they may be much longer in the young wood on old bare trunks. The resistance to transverse flow through saturated wood is 800 to 45,000 times greater than to longitudinal flow, the resistance to filtration under pressure through a single partition wall being from 2 to 10 times greater than that to the flow through the entire length of a vessel filled with water in the wood of a crab apple.

The total resistance to flow in the erect stems of actively transpiring plants appears to correspond to a head of water of from 6 to 33 (shrubs and small trees), or from 5 to 7 (large trees) times the height of the plant. Hence in the tallest trees the total pressure required to maintain active transpiration may be equivalent to as much as 100 atmospheres.

No leaf could produce or maintain an osmotic suction of this intensity, and in the presence of large air-bubbles in the vessels the stress transmitted in them from the leaves could never be as great as an atmosphere. Vines* found, for instance, that the suction force of a transpiring branch was never greater than two-thirds of an atmosphere. The supposition that these forces might summate is entirely erroneous. On the contrary, the leaves at the base of a tree would pull water down from the upper vessels and leaves, instead of up from the roots, in the absence of any pumping action in the stem, and of any root-pressure.

If the air-bubbles in the vessels were exceedingly minute, they might be under a small positive pressure, while the water outside was under a maximal strain of five atmospheres. This would suffice to overcome the resistance offered during active transpiration by 30 to 80 feet of stem, hence the results obtained by Strasburger with dead stems. The maximal osmotic suction exercised by the leaves, as determined by comparing the osmotic pressures during active transpiration of the leaves at the top and bottom of an elm 18 metres high, appears to be from 2 to 3 atmospheres, and is usually less than this. At the same time the total resistance to flow in the trunk of this tree would be from 10 to 12 atmospheres.

It appears, therefore, that to maintain flow, a pumping action of

* 'Annals of Botany,' 1896, vol. 10, p. 438.

some kind or other must be exercised in the wood, for which the presence of active living cells is essential. In support of this it has been shown that the production of wood in a slowly growing tree is greater than is necessitated by mechanical requirements. In other words, the production of new wood is largely determined by the length of time during which the wood-parenchyma can remain active.

There is no known means by which these cells can directly pump water in a definite direction, although the existence of a power of absorbing and exuding water under pressure has been empirically determined to exist in the living wood of cut branches. It is suggested that the wood-parenchyma cells by the excretion and re-absorption of dissolved materials may bring into play surface-tension forces within the vessels of sufficient aggregate intensity to maintain a steady upward flow, and to keep the water of the Jamin's chains in the vessels in a mobile condition ready to flow to wherever suction is exercised upon it.* The rapid rates of diffusion required for such action do actually exist in the wood-parenchyma cells.

It appears that the terminal branches of trees at heights of from 22 to 44 feet above ground exhibit little or no power of bleeding in spring. Possibly in such trees the pumping action is only used or developed in the wood of the older stems, or is only exercised when transpiration is active, and when the water-columns in the vessels attain a definite size relatively to the wood-parenchyma cells. The importance of the Jamin's chain in the vessels is that it renders a staircase pumping action possible, and enables the water to be maintained in the vessels in a labile condition, ready to flow to any point where moderate suction is exercised. This pumping action being diffused and probably regulated, need not produce any high pressure of exudation at the terminal branches of tall trees, which, in fact, appears always to be absent at high levels.

* Surface-tension actions would be possible in the absence of air-bubbles wherever the wood-parenchyma cells contained oil or any other substance non-miscible with water, as they often do.